

A Study of Isolating Mechanisms among Neotropical Butterflies of the Subfamily Riodininae

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Abstract. This paper examines the perching behavior of ten genera of Neotropical riodinine butterflies to determine the nature of perching as a premating isolating mechanism in the context of the tropical forest habitat. The study shows that congeneric sympatric riodinines achieve habitat isolation through mating in different topographic sites and at different times, in addition to displays and pheromones. The study concludes that: 1) perching periods are generally of shorter duration than those of nearctic lycaenids; 2) females actively search out perching sites where they wait for males, when the latter are scarce; 3) spacing of perching sites varies considerably from one genus to the next, as do perching positions; 4) many genera, such as *Nymphidium* have retractable scent hairs, suggesting that pheromones are important as an ethological barrier; and 5) observations of habitat spacing have considerable taxonomic value.

Introduction

The purpose of this paper is to examine the perching behavior of congeneric riodinine butterflies to determine the nature of perching as a premating isolating mechanism, and the adaptation of this mechanism to the neotropical forest habitat.

Most of the studies of butterfly mating behavior to date have dealt with Nearctic species or with the larger Neotropical butterflies, such as heliconids or nymphalids, whose behavior is more likely to be patrolling than that of perching. The mating behavior of smaller sized butterflies, such as riodinines have been treated in a general way only by Ebert (1967) and Callaghan (1977, 1978). Additional information on this group is spotty at best. Shields (1967), for example, quotes Keith Brown to the effect that many riodinine species hilltop near Rio de Janeiro. No studies to date have examined Neotropical riodinine perching behavior as a premating isolating mechanism.

The following discussion treats the methods used in the study, followed by a description of the different types of riodinine perching localities, the perching habits of ten genera of riodinines, and concludes with a discussion of the nature of riodinid premating isolating mechanisms.

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Methods

The present study is based on five years of observations of riordinine behavior in many localities, from Southern Brazil to Colombia and Panama. Ten genera and 36 species are treated in the present study. These genera were chosen among many observed because of the relatively large number of observations in each case, and/or because of the greater number of congeners flying in the same area, and finally, because they were representative of variation in riordinine perching behavior generally. An overall survey of mate locating strategies among riordinines will be included in a forthcoming paper.

I recorded the times, location, and perching position of each observation in the field on a portable tape recorder. On numerous occasions I captured the perching butterfly to make a positive identification. At other times, when I became better able to recognize the perching species from a distance, I would not capture the insect, but note the time and place as usual. If later I returned to the same spot and observed the same or another individual of the same species, I recorded it as a second observation. The times given in the paper are on a 24 hour basis.

As I observed few cases of copulating riordinids, I had to develop a method of distinguishing perching from resting butterflies. Perching behavior is defined as "males resting at characteristic sites and investigating passing objects by flying out at them in search of females" (Scott, 1975). Thus, perching butterflies are always associated with a particular time and place. The problem was to determine the time and place of the perching activity. This I solved by making multiple observations for each species. Species were not included in the study for which the data were too few and/or too widely spread in space and time. Secondly, perching male riordinids often displayed an aggressive attitude towards their own species and towards other butterflies passing by. If they were disturbed, they would eventually return to the same spot. This behaviour is very distinct and hard to confuse with riordinids merely moving through an area.

Study Area Description

For the purpose of grouping the field observations, I divided the riordinid perching sites into two major categories, and eight sub categories. The two principal ones were forests and hilltops. Forests were subdivided into "outside woods edge", "on woods edge", "treefalls", "inside woods edge", and "sunflecks", designated by the letters "A, B, C, D, and E", respectively. Hilltops were divided into three categories: "hilltop sunflecks", hilltop treefalls", and "open hilltops", referred to as "F, G, and H", respectively. A detailed description of each of these perching sites is as follows:

FORESTS.—The great majority of the riordinids are forest butterflies inhabiting the Amazon and Orinoco drainages. As most of the land area is

relatively flat and forested, the rioidinid forest butterflies have compensated for the lack of prominent topographical features by substituting microhabitats within the forest itself based on sunlight/shadow and the time of day. I have designated five of these, as illustrated in figure 1 and discussed below, in order of decreasing solar exposure.

A. Outside Woods Edge.—The tropical forest is far from being a homogeneous mass. It is frequently cut by rivers, streams, campos, and cerrados which delineate definite "woods edge" situations, where the forest stops and another medium begins. Forest species will sometimes be found perching here up to 30-40 meters from the forest margin, usually in the early morning when the first rays of the sun strike the area, to about

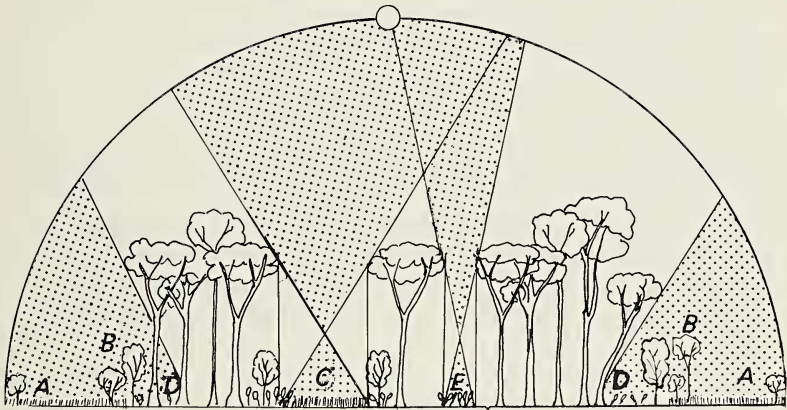


Fig. 1. FOREST PERCHING LOCALITIES

The different forest perching localities described in the text are illustrated in the schematic drawing above. The sun moves in an arc from right to left, illuminating the different localities, shown by the letters A, B, C, D and E.

800 hours, when the day starts to get hot, and again in the late afternoon, from about 1600 hours to sunset. Males perch on small bushes or other prominent foliage and chase each other vigorously around the area.

B. On Woods Edge.—In this perching site, the butterflies rest on the outer edge of the forest, usually on or under leaves which shine in the sunlight.

C. Treefalls.—Inside the forest, there are significant openings in the canopy through which enough sunlight penetrates to stimulate the growth of plants usually associated with more open areas, such as *Solanum* and various grasses. Young trees from three to four meters high sometimes crowd these areas. This habitat may be caused by a treefall, a logging road, or a small creek. The maximum size of these areas is a height-width ratio of 3:2 at right angles to the path of the sun, as illustrated in figure 1. Areas

with a height to width ratio greater than this fall into categories A and B above.

D. Inside Woods Edge.—The rays of the late morning or afternoon sun often penetrate the forest edge to strike areas up to six meters inside the forest, “spotlighting” certain foliage, which mark the riodinid perching sites.

E. Sunflecks.—Small breaks in the forest canopy allow the sun to penetrate to the forest floor for a few minutes each day, creating a small patch of light, or “sunfleck”. This small amount of direct sunlight encourages the growth of broad leaved shade plants, such as *Heliconia* and various *Philodendron* which, when the light strikes them, contrast sharply with the normally barren aspect of the forest floor. These leaves serve as preferred perching localities for many species of forest riodinids, especially during the early afternoon hours. The height to width ratio for this site is at least 5:1.

HILLTOPS.—To the north, west, and south of the Amazon-Orinoco drainage, the topography becomes more accentuated and hilltops more prominent as sites for mate locating. Hilltops are defined as accentuated topographic features from which the ground drops away on all sides. They may be located on ridges, but the rule still holds, just that on one or two sides the ground does not drop away as fast as on the others. I define three different hilltop situations, which are illustrated in figure 2.

F. Hilltop Sunflecks.—Small breaks in the canopy of a forested hilltop



Fig. 2. HILLTOP PERCHING LOCALITIES

In the schematic drawing above, the hilltop perching localities H, G, and F described in the text are illustrated.

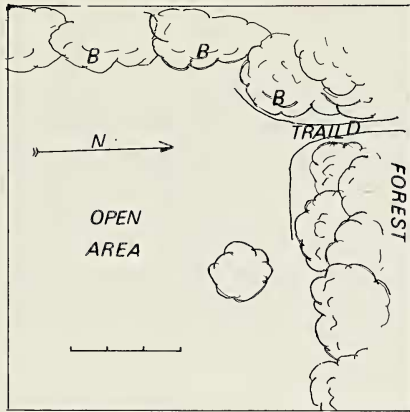


Fig. 3. PERCHING CORNER

The letters refer to sites where perching riordinids await mates during the morning hours. The scale is in meters.

create perching sites where the sun strikes prominent leaves near the forest floor.

G. Hilltop Treefalls.—This category is basically the same as “D” above, except that it occurs on hilltops. Openings in the canopy can be caused by wind felled trees, or human intervention.

H. Open Hilltops.—These are found in open forest or savanna formations. The ground cover is composed of grasses, small bushes, and/or with a few widely spaced trees. Most of the hilltops in the Brazilian cerrado are this type.

At times, categories G and F may not correspond to the topographically highest spot on a hill, especially if there has been considerable alteration of the hilltop forest.

Finally, the question arises as to where the riordinids perch within the more open localities discussed above, namely sites B, C and D. In my experience, perching usually takes place in what I call “perching corners”, illustrated in figure 3. These consist of an opening in the forest, usually in the shape of a corner, or funnel, when viewed from above. Perching butterflies await at the end of the funnel for members of the opposite sex. This behaviour suggests that in forest localities B, C and D mate seeking butterflies of either sex are attracted by lighter areas along the forest edge, along which they move until they become “trapped” in the corner where mates can be found waiting. Figure 3 shows the locations of midmorning perching riordinids in a perching corner, on the side on which the morning sun was striking. The north, or shaded side was without perching activity. Perching corners may be in bold relief, such as the one depicted, or merely a bush which protrudes slightly further from the edge of the forest. However, the existence of a corner appears to be relevant in all cases.

Results

The perching data for each of the ten genera was placed on graphs, figures 4 through 8, with the hours of the day on the horizontal axis, and the eight perching localities on the vertical axis in accordance with the solar exposure. Midday is shown by a vertical line. The range of the observations for each species is shown by a horizontal line, starting with the hour of the first observation and ending with the last. The total number of observations for each species is also shown on the graph. The hilltopping localities were also included, as I found that in several cases congeneric species were not relegated to only forest or hilltop, but both.

Genus *Euselasia* Figure 4

Five species fly together in the Xerem reserve near Rio de Janeiro, Brazil. That I found *E. hygenius* (Stoll) and *E. thucydides* (Fabricius) perching in the same site might suggest that spacing was imperfect for the *Euselasia*. However, the phenotypes of *hygenius* and *thucydides* are morphologically quite different. Phenotypically, *thucydides* is similar to *E. utica* (Hewitson), and *E. crinon* Stichel is close to *E. hygenius*. It is these two pairs of species which show the greatest spacing in the habitat.

When perching, the *Euselasia* rest on the underside of leaves with their wings folded over their backs. I have encountered female *Euselasia* rarely, but have on occasion found them frequenting male perching sites at the same time of day.

Genus *Alesa* Figure 4

At Villavicencio, Meta, Colombia, two species of the genus *Alesa* may be found hilltopping. I have always observed *A. prema* (Godart) perching on hilltops from central Brazil to Colombia. *Alesa amesis* (Cramer) flies throughout the Amazon drainage and perches in type C and E localities in the forest. Villavicencio is the only locality where I have found *amesis* perching on hilltops. Both species rest with their wings outspread on the upper surfaces of leaves on the hilltop, although *amesis* also rests on the undersides of leaves when perching in the forest. Certain colors and wing patterns may be significant in attracting females of these two species. *Alesa prema* males perch in sunny localities which emphasize the brilliant green upper surfaces of the wings, while *A. amesis* males perch in shaded areas which form a marked contrast with the brilliant white tips of their antennae. Both species demonstrate significant spacing of perching sites and times.

Genus *Ancyluris* Figure 5

Five species of this genus fly in the Villavicencio area in Meta, Colombia. All five male phenotypes are very similar in appearance, the upperwing surfaces having a red band running from the costa of the forewing to the

FIGURE 4

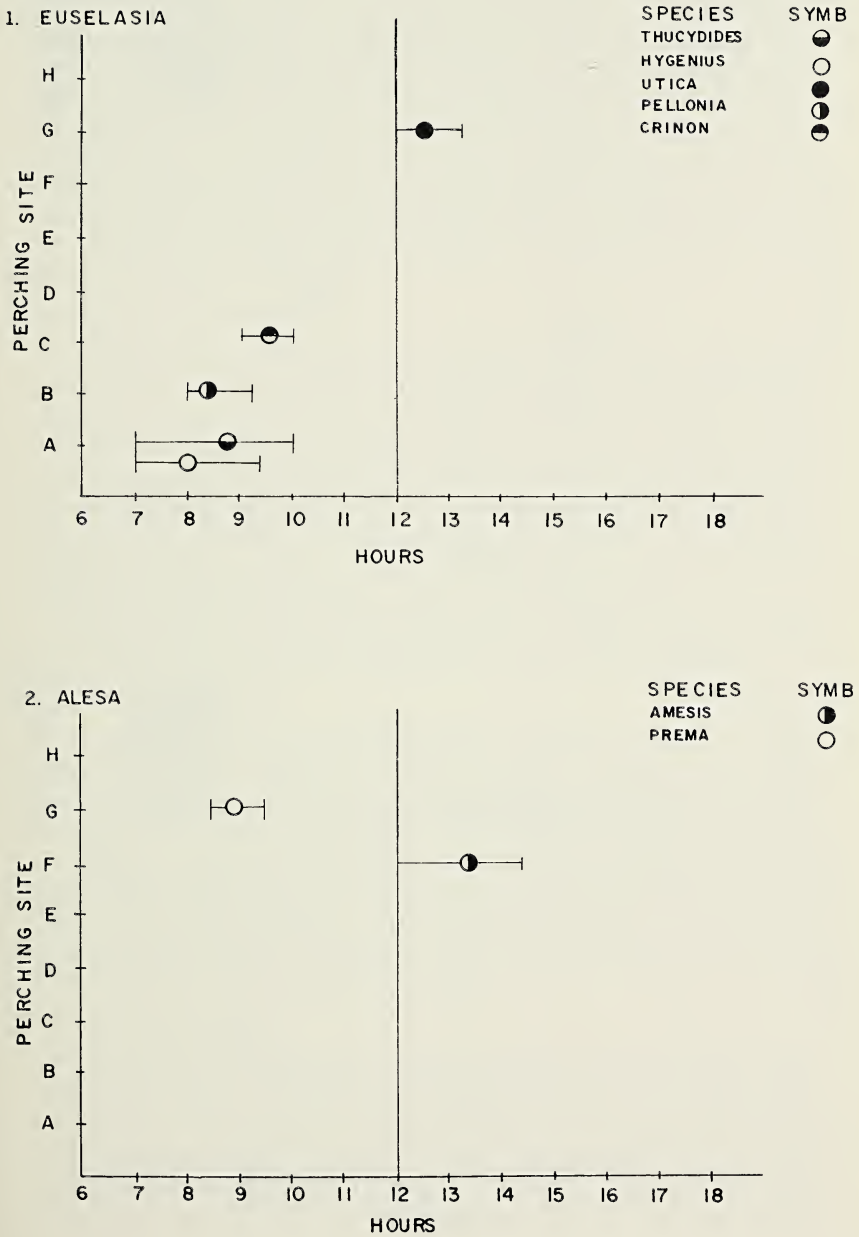
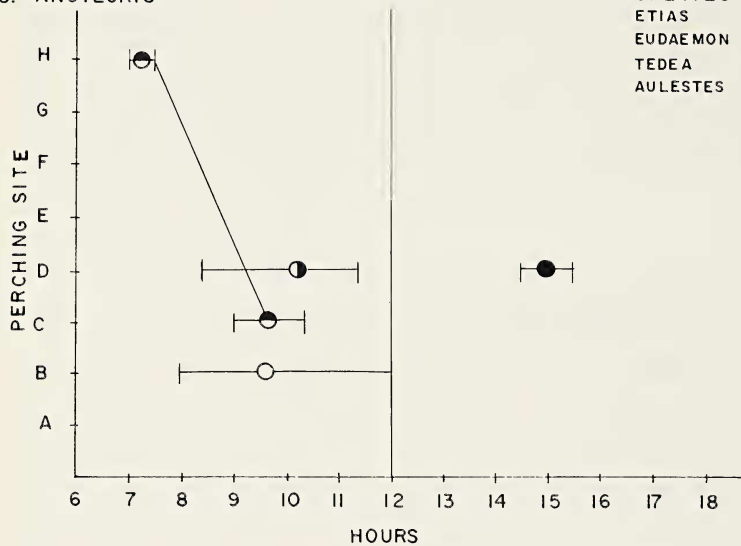


FIGURE 5

3. ANCYLURIS



SPECIES

ETIAS

EUDAEMON

TEDEA

AULESTES

SYMB

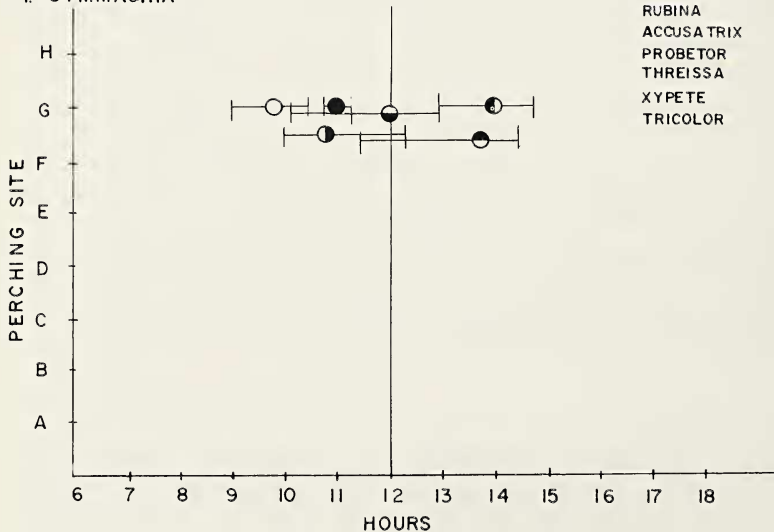
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4. SYMMACHIA



SPECIES

RUBINA

ACCUSATRIX

PROBETOR

THREISSA

XYPETE

TRICOLOR

SYMB

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anal angle of the hindwing, and the undersides of the wings displaying a brilliant metallic blue color. However, the female phenotypes of these species are quite different. All these species show significant spacing within the habitat. One, *A. tedeia* (Cramer) perches on open hilltops at daybreak then inside the woods edge later in the day. Perching height differs somewhat between species. *A. eudaemon* Stichel perches three to five meters off the ground. *A. aulestes jocularis* Stichel and *A. tedeia* rest at heights from one to two meters, *A. etias* (Saunders) less than one meter, and sometimes on the ground. All the species normally perch on the upper surfaces of the leaves with wings flat. Although I have rarely encountered females, I have observed them frequenting male perching sites at the same time of day as the males, which provides an excellent clue as to which females belong to which males.

Genus *Symmachia* Figure 5

I observed six species currently placed in the genus *Symmachia* hilltopping at Gamboa, Panama. All perch in a type G locality, and various species may fly at the same time. Thus, it would seem that here the breakdown of spacing in the habitat would be complete. However, if the four typical *Symmachia* having the strongly arched costa of the forewing are separated from *S. asclepia xypete* (Hewitson) and *S. tricolor* Hewitson, which do not, the spacing once more becomes apparent. The foregoing suggests that the current taxonomic status of the genus *Symmachia* may not in fact reflect the biological status of these butterflies.

The members of this genus are very fond of hilltops, and rest while perching on the undersides of leaves with their wings outspread.

Genus *Charis* Figure 6

Two species of *Charis* fly sympatrically beside the Rio Negro in Meta, Colombia. I have observed *C. auius* (Cramer) perching in the early morning in type A localities. Later, this species is encountered in D sites. *C. cleonus* (Cramer) males perch in E localities during the afternoon, usually up to three in number, chasing each other around in a tight circle in the sunfleck. Both species rest while perching on the upper surface of a leaf with their wings outspread. I have observed females of both species frequenting the male perching sites, but in smaller numbers and only at times when the males appear to be rarer.

Genus *Anteros* Figure 6

I recorded the perching habits of three sympatric species of *Anteros* near Felixlandia, Minas Gerais, on the Brazilian Planalto. An undescribed subspecies of *A. carausius* Westwood hilltops during the midmorning. *Anteros formosus* (Cramer) is always found in the early afternoon on or just inside the edge of the gallery woods, and *A. lectabilis* Stichel perches in the late afternoon in the more open cerrado and campos. All three species rest

FIGURE 6

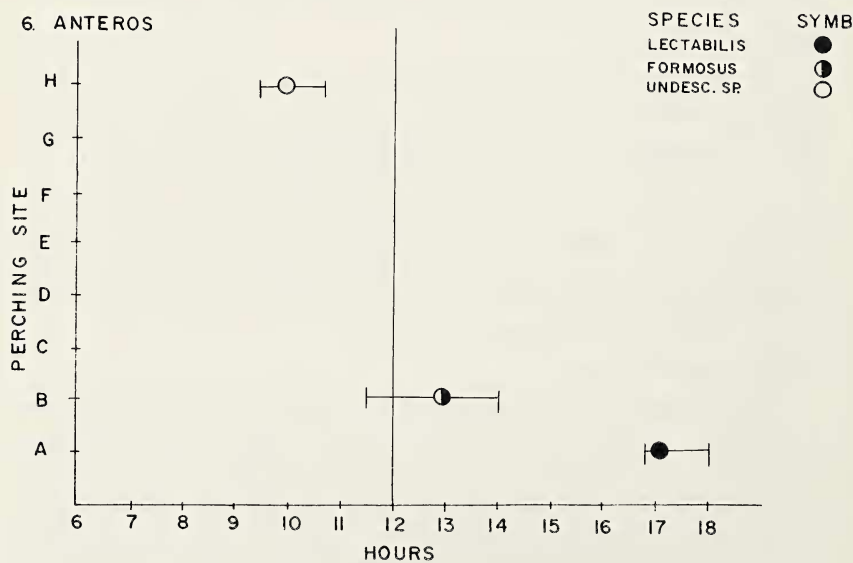
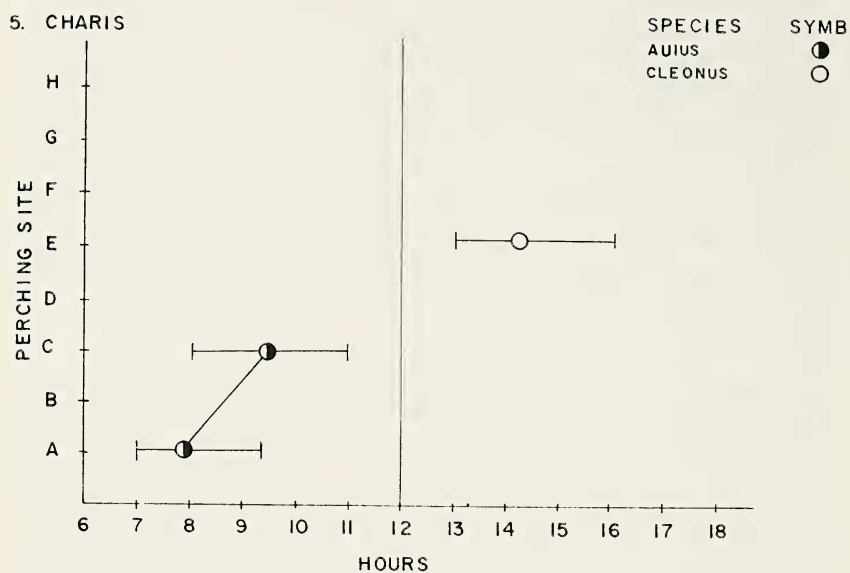
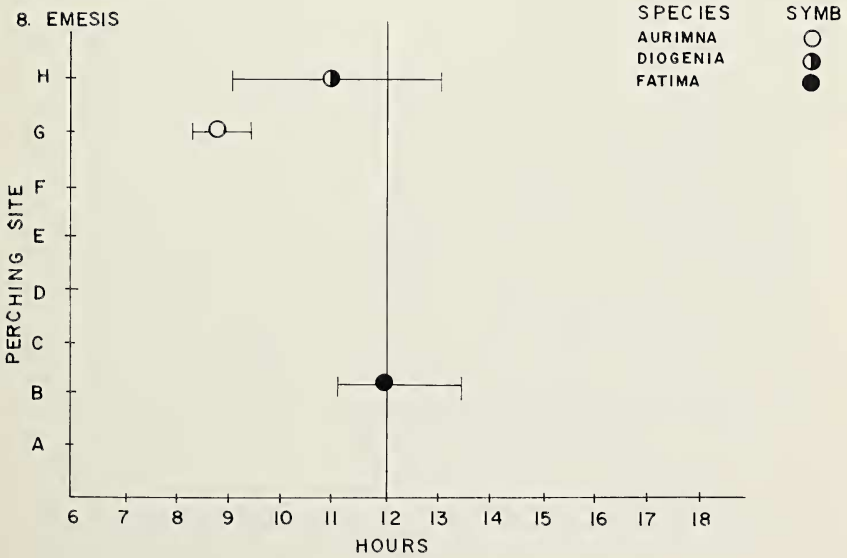
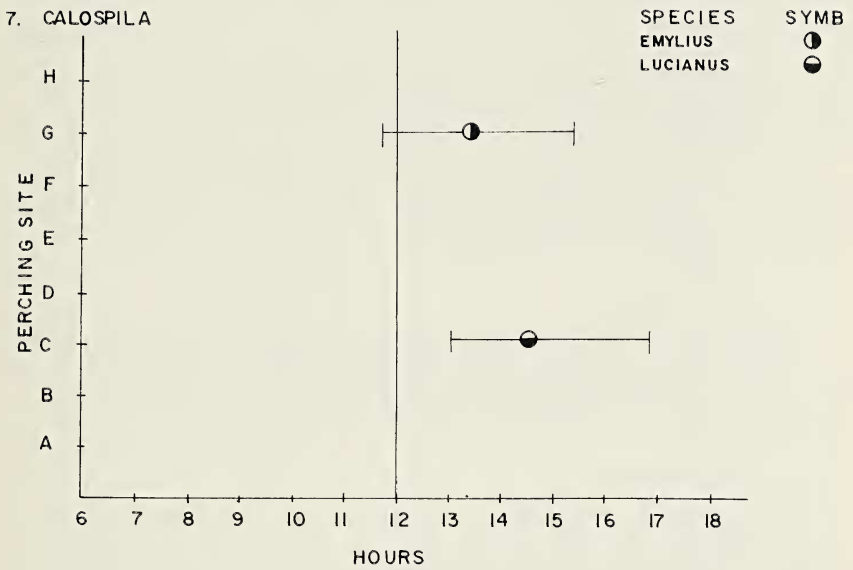


FIGURE 7



on the undersides of leaves with their wings folded over their backs. To date I have only observed the males perching. The females appear to be much rarer.

Genus *Calospila* Figure 7

Two closely related species of the genus *Calospila* fly near Villavicencio, Meta, Colombia. I found *C. emylius* (Cramer) males on hilltops in numbers of up to 12 individuals during the afternoon. On other occasions, when the males were less common, I found females frequenting the same sites at the same times. *C. luciana* (Fabricius) also perches during the afternoon, but always in woods edge localities. Both species rest under leaves with their wings outspread.

Genus *Emesis* Figure 7

At Villavicencio, I observed three species of the genus *Emesis* perching, all of which demonstrate spacing in the habitat. All these species rest on the upper leaf surfaces with their wings flat, and from one to three meters off the ground.

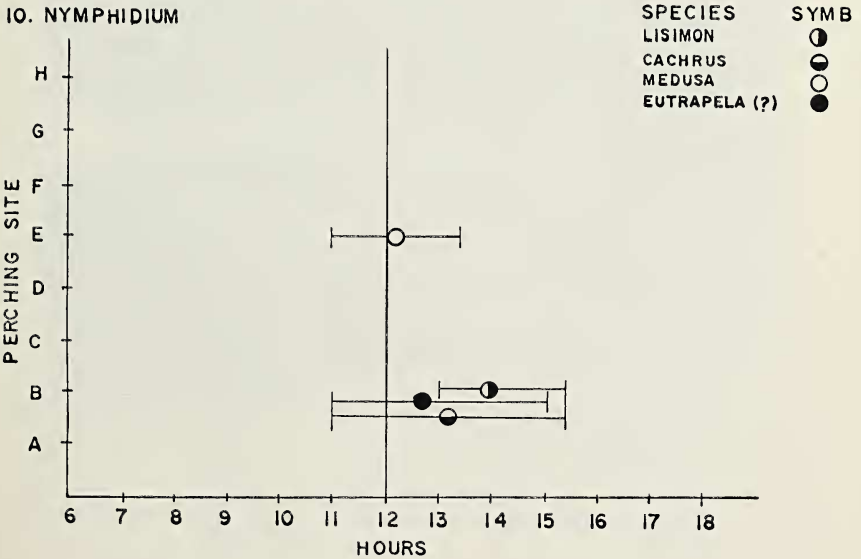
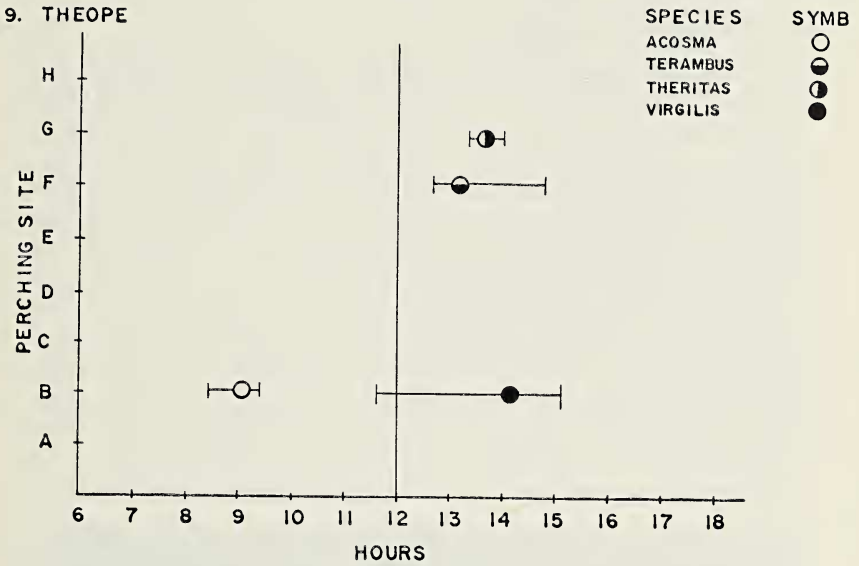
Genus *Theope* Figure 8

Four species of the genus *Theope* are sympatric near Villavicencio. I have found *T. theritas* Hewitson and *T. terambus* (Godart) perching in very similar localities, but never together. After repeated observations I concluded that *T. theritas* perches in slightly more open areas than *terambus*. All the species of this genus rest on the undersides of leaves with their wings over their backs.

Genus *Nymphidium* Figure 8

Four species of the genus *Nymphidium* are sympatric in the Villavicencio area. Three of them, *N. cachrus* (Fabricius), *N. lisimon* (Stoll), and *N. estrapela* (?) Bates may on occasion be found perching together in type B and C localities. There is no doubt that these three butterflies are valid species, as there are distinct genetical and other morphological differences between them. This would appear contrary to the contention that congeneric species space themselves throughout the habitat. However, dissection of the male genitalia of these butterflies reveals scent hairs on the last abdominal segment (Fig. 9). Through observing live specimens, I have discovered that these scent hairs can be extended and retracted much like the hair pencils of certain Danainae. The existence of these organs suggests that pheromones may be important among the *Nymphidium* as a barrier to interspecific mating. Similar organs are found on other closely related genera, such as *Synargis*, *Juditha*, and *Audre*. What most of these butterflies have in common is that they inhabit open forest formations and savanna which lack the variety of light/shadow combinations found in the forest. The use of pheromones may compensate for this

FIGURE 8



lack of habitat variety among these genera. These structures are also found in the genus *Stalachtis* which inhabit deep woods, are mimetic, and slow flying (Keith Brown, pers. comm.).

Discussion and Conclusions

The biological properties which prevent the interbreeding of closely related species have been called "isolating mechanisms" since 1937 when Dobzhansky first used the term. These mechanisms were defined by Mayr (1963) as "biological properties of individuals which prevent the interbreeding of populations which are actually or potentially sympatric." Mayr went on to divide isolating mechanisms into two categories; premating, which prevent interspecific crosses and postmating, which reduce their success. He subdivided premating into three parts: a) potential mates do not meet due to seasonal or habitat isolation, b) potential mates meet, but do not mate due to behavioural (ethological) isolation, and c) copulation is attempted but no transfer of sperm takes place due to mechanical differences. Mayr went on to state that habitat isolation is unimportant in mobile animals, and that seasonal isolation is poorly known. In his opinion, the most important mechanisms were behavioural (ethological).

Studies of the mating behaviour of butterflies published since then have

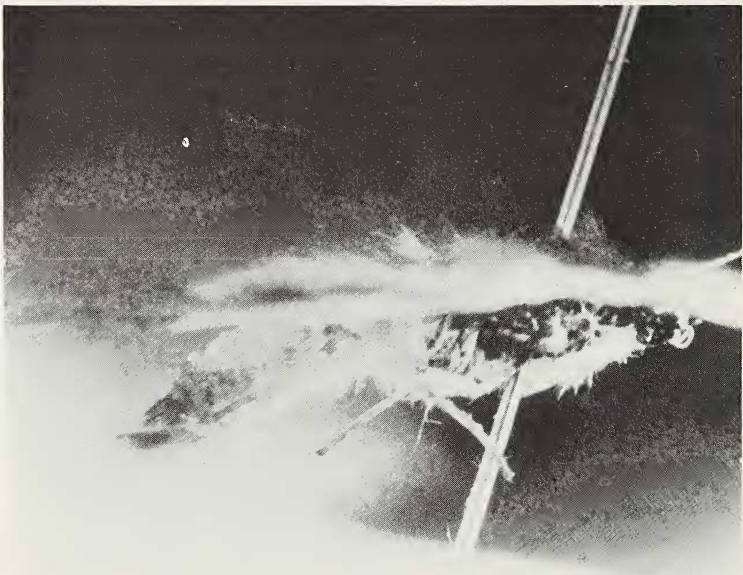


Fig. 9. Dried specimen of male *Nymphidium cachrus* with abdominal scent hairs extended.

shown that partial habitat isolation has been accomplished through mating in different topographic sites within the habitat and at different times. Scott (1975) recorded 18 congeneric pairs of sympatric nearctic butterflies mating in different sites, which included ridges, hilltops, and gullies. Shields (1967) and Scott (1968) examined hilltops as mating sites for many species of butterflies. That many species mate during restricted times of the day has long been recognized by many workers (Miller & Clench, 1968; Scott, 1975; Shields & Emmel, 1973).

The data presented in this study regarding the perching habits of congeneric sympatric species of riodinid butterflies suggest that riodinids have developed a series of complex premating mechanisms in order to maintain specific isolation within the habitat. These mechanisms appear to be in two stages. In the first, similar phenotypes of sympatric species divide the forest habitat into rendezvous sites, defined by different topographic physical features; by light/shadow contrast, and by different hours of the day. The second stage consists of a number of varied ethological barriers, such as displays, and/or pheromones. If for some reason the space/time mechanism fails, then the second stage of ethological mechanisms comes into play.

Scott (1968) and Shields (1967) confirmed that perching and hilltop species are those which have low density populations, and which feed on low density foodplants. These observations characterize most neotropical forest butterflies (Ebert, 1967), and particularly riodinids (Callaghan, 1977, 1978). Scott and Shields also postulated that through the use of rendezvous localities, rarer species could more easily find mates, and through perching for relatively short periods, could keep exposure to predation to a minimum. My observations on riodinid perching habits support this assertion. The fact that riodinid perching was observed at specific times and places attests to the adaptive significance of perching. Through the spacing of perching times and sites throughout the habitat these butterflies save much time, exposure, and effort in avoiding interactions and attempted matings with closely related species.

The data presented in this study suggest a number of conclusions regarding riodinine perching.

I. Riodinines perch for relatively short periods during the day. The average perching periods of each genus are shown in the following table:

Genus	Average Duration of Perching (tenths of hours)
<i>Euselasia</i>	1.9
<i>Alesa</i>	1.3
<i>Ancyluris</i>	2.9
<i>Symmachia</i>	2.8

Genus	Average Duration of Perching (tenths of hours)
<i>Charis</i>	2.8
<i>Anteros</i>	1.3
<i>Calospila</i>	3.3
<i>Emesis</i>	2.4
<i>Theope</i>	1.8
<i>Nymphidium</i>	3.4
Average of 10 genera	2.4

The above perching periods are short compared to Nearctic lycaenidae, most of which perch "all day" (Scott, 1975). Notable exceptions in Scott's study are *Apodemia nais* and *Apodemia mormo* which perch from 1130 to 1430 and 1100 to 1430 hours, respectively. On the other hand, the average lifespan of Neotropical riodinines appears to be longer (Callaghan, 1978), which suggests that on the balance, time devoted to mate location over the lifetime of both Nearctic and Neotropical Lycaenids may be similar.

The average perching duration observed of 2.4 hours per day is probably close to the actual average. While some riodinines perch in different habitats at different times, such as *Ancyluris tedeia* and *Charis auius*, this seems to be the exception, for continuous observation of all micro habitats in the study areas failed to reveal similar activity by other species. Although I have always made it a point to search the forest canopy, I have never discovered riodinine activity there. The perching duration of hilltopping species is easily measured, as is that of species which perch in open areas. The perching duration of species that perch in D and E areas are harder to determine due to the tendency of these species to move to other sunflecks once the first disappear into shadows. However, in the present study, only four out of 36 species frequented D and E areas.

II. Females will be found frequenting male perching sites. They were never observed to perch in the male fashion, aggressively investigating passing butterflies, nor interacting with each other. In fact, the only way to tell whether the females were actually perching was that the males of the same species had been observed perching at the same time and place. The females were observed rarely, and usually on occasions when the males were scarce. These observations suggest that females actively search out rendezvous sites for mating, and do not just "happen by". This behaviour would eliminate the need for elaborate female rejection rituals, as found in some pierids and heliconids, because females enter the rendezvous areas when they are receptive to mating, and do not when they are not, saving time, energy, and exposure for both sexes.

III. The relative spacing between rendezvous sites varies considerably between congeneric sympatric species. Some genera show extremely wide

spacing, such as *Euselasia*. Others, such as *Ancyluris* and *Charis* may have species which perch at different sites at different times. At the other extreme, some *Theope* species perch in sites with slight differences and different *Nymphidium* species frequent similar, and sometimes the same sites. In the case of *Nymphidium* other ethological factors, such as chemical signals, seem to be of greater importance.

IV. Perching position shows considerable variation between genera. Displays by males are apparently important in *Alesa*, *Emesis*, *Charis*, and to a lesser extent in *Nymphidium*, due to the tendency of these groups to perch on the upper leaf surfaces with wings outspread. The remaining genera hide under leaves at the perching sites. *Euselasia* and *Theope* have cryptically marked and colored undersides of the wings, with eyespots and/or leaf markings. Relative perching height may be an important factor for some genera, such as *Ancyluris*, but the data gathered for the other genera in this respect are inconclusive.

V. The prominence of scent hairs in the *Nymphidium* and related groups suggest that pheromones probably play an important role as an ethological barrier to interspecific mating. The majority of the *Nymphidium*, *Synargis*, and *Juditha* perch for long periods in the same type of open habitat. Encounters between congeneric species must be common. I suggest that genera which perch in habitats which do not afford the variety of light/shadow and topographic site combinations depend more upon ethological mechanisms for species recognition than do strictly forest dwelling groups. A third strategy found among savanna dwelling groups such as *Audre*, *Calephelis*, and *Apodemia*, is that of forming colonies about their foodplant. This strategy will be examined in detail in a forthcoming paper (Callaghan, in prep.).

VI. Observations of the spacing of butterflies in a habitat can be of considerable taxonomic value. The genitalia of many closely related riodinid phenotypes are practically identical, as are other morphological characters. Observations on spacing provide many clues not only as to the systematic relationships between questionable phenotypes, as illustrated in the case of *Symmachia*, but as to the sexing of dimorphic species, such as *Ancyluris*. In my opinion, no systematic survey of any group is complete without field observations of habitat spacing.

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Literature Cited

- CALLAGHAN, C. J., 1977. Studies on resting a butterflies. I. The life cycle and immature biology of *Menander felsina* (Riodininae), J. Lep. Soc. 31:173-182.

- _____, 1978. Studies on resting butterflies II. Notes on the population structure of *Menander felsina* (Riodinidae). J. Lep. Soc. 32:37-48.
- EBERT, H., 1969. On the frequency of butterflies in eastern Brazil with a list of the butterfly fauna of Pocos de Caldas, Minas Gerais. J. Lepid. Soc. 23, Suppl. 3, 48 pp.
- DOBZHANSKY, T., 1937. Genetics and origin of species. 1st ed. Columbia University Press, New York.
- FERRIS, D. D., 1967. Some additional notes on mating behavior in butterflies. J. Lep. Soc. 23:271-272.
- MAYR, . 1963. Animal species and evolution. Belknap Press, Harvard Univ., Cambridge, MA.
- MILLER, L. & H. CLENCH, 1968. Some aspects of mating behavior in butterflies. J. Lep. Soc. 22:125-132.
- SCOTT, J. A., 1968. Hilltopping as a mating mechanism to aid the survival of low density species. J. Res. Lep. 7:191-204.
- _____, 1972. Mating of butterflies. J. Res. Lep. 11:99-127.
- _____, 1973. Adult behavior and population biology of two skippers. J. Res. Lep. 12:181-196.
- _____, 1974. Population biology and adult behavior of *Lycaena arota* (Lycaenidae). J. Lep. Soc. 28:64-72.
- _____, 1975. Mate locating behavior of the western North American butterflies. J. Res. Lep. 14:1-40.
- SHAPIRO, A. S., 1975. The temporal component of butterfly species diversity, pp. 181-195. In: Cody, M. L. & J. Diamond, eds., Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA.
- SHIELDS, O., 1967. Hilltopping. J. Res. Lepid. 6:69-178.
- _____, & J. EMMEL, 1973. A Review of carrying pair behavior and mating times in butterflies. J. Res. Lep. 12:25-64.